

The University of Chicago

HISTOLOGICAL RESPONSES OF
CABBAGE PLANTS GROWN AT DIFFERENT
LEVELS OF NITROGEN NUTRITION
TO INDOLE(3)ACETIC ACID

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

DEPARTMENT OF BOTANY
1938

By
ETHEL GOLDBERG

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Reprinted from
THE BOTANICAL GAZETTE
Vol. 100, No. 2, December 1938

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HISTOLOGICAL RESPONSES OF CABBAGE PLANTS GROWN AT DIFFERENT LEVELS OF NITROGEN NUTRITION TO INDOLE(3)ACETIC ACID

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 495

ETHEL GOLDBERG

(WITH TEN FIGURES)

Introduction

Considerable histological work has recently been done on the responses of various plants to applications of growth promoting substances. FISCHNICH (3) worked with *Coleus*; KRAUS, BROWN, and HAMNER (9), HAMNER and KRAUS (7), and LINK, WILCOX, and LINK (11) with bean; BORTHWICK, HAMNER, and PARKER (2) with tomato; HARRISON (8) with *Iresine*; and HAMNER (6) with *Mirabilis*. All reported great stimulation of various tissues, resulting in the production of callus and root primordia. GREENLEAF (5) noted the production of shoots from the cut surface of *Nicotiana* treated with indole(3)acetic acid, but reported no histological work. BEAL (1) made a detailed study of bud development from leaf axils in *Lilium harrisii* induced by applications of indole(3)acetic acid to the cut surface of the decapitated stem.

Cabbage was found to be very responsive to indole(3)acetic acid, and to produce shoots from the decapitated surface of a large proportion of treated seedling stems (4). It was also noted that the reaction of the plants, at least in rate, to applications of this substance was largely dependent upon the nutritive state of the plant. These observations were made the basis of the anatomical study reported here.

Material and methods

About 2000 young cabbage plants of the Wisconsin All Seasons variety were used throughout the experiments. All were grown under ordinary greenhouse conditions of light and humidity. Some were grown in soil, while others were grown in sand in the Chicago

soil-temperature nutrient tanks, which maintain the root temperature at 20°C . with a variation of only 1° in either direction. There was an average diurnal range in greenhouse temperature of 13°C . (24° to 37°C .). The plants in sand were watered each day with either Shive's R_2S_5 nutrient solution, or the same solution in which the calcium nitrate had been replaced by calcium chloride.

A 3 per cent mixture of indole(3)acetic acid (Merck) in lanolin was used for all applications. Material for histological work was collected at intervals of 6 hours for the first 72 hours; every 12 hours for the next 144 hours; and every 24 hours thereafter until 504 hours had elapsed. It was fixed in Navashin's solution and imbedded by the butyl alcohol-paraffin method. Sections were cut at 12μ and stained with triple stain.

Experiments and results

SEEDLINGS GROWN IN SOIL

DECAPITATED FIRST INTERNODES.—Seedlings 20 days old grown in ordinary greenhouse soil were cut squarely across near the top of the first internode. The cut surface was then smeared with the indole(3)acetic acid mixture. Controls were smeared either with lanolin or were left with no treatment other than decapitation.

At the time of treatment the stems had just begun to undergo secondary thickening (fig. 2A). A well defined epidermis and cortex have developed, the outermost cells of which contain abundant chloroplasts. The endodermis can be distinguished from other cortical cells, although with difficulty, by the denser cytoplasm and somewhat more prominent nuclei. Sieve tube and companion cells of the primary phloem are mature, and one or two rows of pericyclic cells still showing protoplasmic content cap each phloem group. The cambium is just beginning its activity, with not more than two rows of as yet undifferentiated cells on either side. Prominent xylem rays are apparent in some of the larger bundles. The pith is large in extent, with comparatively narrow medullary rays passing between the bundles.

Within 18 hours after treatment, cell enlargement in the pith is apparent. By the end of 24 hours, the cortical cells also show an

enlargement. After 54 hours the size of these cells has almost doubled, and epidermal cells have also enlarged to keep pace. This is the maximum enlargement of individual cells of the pith; occasionally some cortical cells in later stages may almost triple their size.

By the end of 30 hours an increase in the activity of the cambium and a delay in maturation of its derivatives are apparent. The endodermis is much more easily identified, owing to the increased density of the cytoplasm and prominence of its nuclei. Many of the phloem parenchyma cells enlarge, and these, together with primary xylem parenchyma, rays, and a few pith cells adjacent to the protoxylem points, show dense cytoplasm and very prominent nuclei. An increased density of protoplasm is also apparent in some of the pericyclic fibers, but it is doubtful whether they play any part in further activity within the stem.

First divisions in the endodermis appear in 42 hours. These may be in any plane, and within 48 hours some cells have undergone division into three, while others are multinucleate. The outermost cells of the medullary and bundle rays divide rapidly and their derivatives increase in size until they push aside the inactive pericyclic cells. There is some division in the primary phloem and the cortex.

Within 60 hours the sites for development of later root primordia have been determined owing to the extremely rapid division of the ray cells and the somewhat less rapid, but nevertheless marked, division of the phloem parenchyma. Certain of the endodermal cells have divided into as many as four (fig. 2*B*), which form a cap over the dividing ray cells. Pericyclic cells are dispersed and in some cases the phloem cells thus come to lie next to the endodermis. The primary phloem cells become crushed.

At the end of 144 hours the histogens of the root primordia have become organized, mainly from ray tissue flanked by phloem derivatives. A cap of endodermis 3–6 layers of cells wide is pushed outward by the growth of the root, which soon pushes through the cortex and epidermis (fig. 3*A*).

Numerous xylem elements mature, some of which differentiate back to abut against the secondary xylem cells of the stem. The xylem parenchyma proliferates to the extent that the original pro-

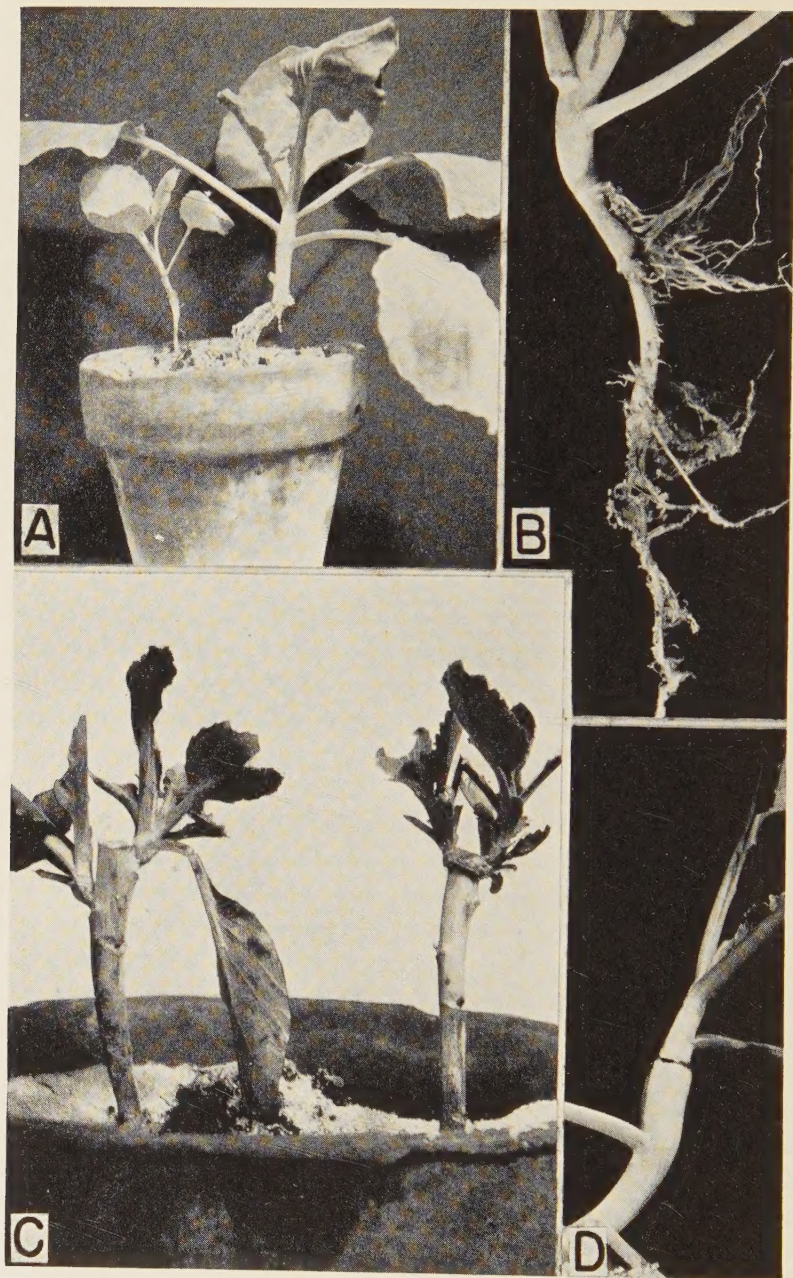


FIG. 1.—*A*: +N and -N control plants showing gross differences 1 week after treatment of other plants of series. *B*: +N plant 3 weeks after placing small daub of lanolin mixture on unwounded internode and covering with sand. *C*: decapitated plants 3 weeks after wounding; plant on left untreated; one on right smeared with lanolin mixture. *D*: unwounded internode 4 days after ringing with fine thread of lanolin mixture. Ink circle drawn on site of application just before photographing.

toxylem points are dispersed. The parenchyma of the proximal parts of the rays, together with the adjacent pith and the pith adjoining the protoxylem points, proliferate greatly, producing a confused array of vascular strands, disorganized tracheids, and highly meristematic areas which may be circular, semicircular, or straight, and oriented in any direction. The vascular strands produce mainly xylem elements with a few irregularly placed phloem cells. Large mounds of callus are usually produced, mainly by the phloem. Root primordia in large numbers are produced only in the region of the original stem, below the callus. They are usually fasciated.

The vascular tissue maturing in the callus at first differentiates downward and connects with the vascular tissue of the root primordia. Usually only disjointed groups of vascular tissue are apparent later. These may be large, or so small as to consist of only one tracheid. The large groups may have very well developed cambiums which run in any direction and then abruptly end. The whole presents a picture of extreme confusion.

About one-third of the plants investigated produced shoots as well as roots, although in such cases the number of roots was greatly reduced (figs. 3*B*, 4, 5, 6). Shoots arise either laterally from tissues outside the vascular bundles which have been stimulated by the indoleacetic acid or from the callus over the surface of the cut end. No plants were noted which produced both lateral and apical shoots. Several shoots of either kind were produced by one plant, as many as ten having been counted on an individual stem. There appears to be no functional difference between shoots produced in either position, the only difference being in point of origin. The lateral shoots orient themselves in an upright position; and since they are located so close to the apical end, after some little growth they cannot be told apart from the others except with great difficulty.

Shoots arising laterally (fig. 4) are initiated by rapid cell divisions, either in the central or innermost cell layers of the cortex or in the rays. Since they originate in the region of the stem which produces adventitious roots, in the earliest stages they cannot be distinguished from young roots except that they do not have a cap of endodermis. In their outward growth, tissues in their path are crushed, and when about to emerge through the epidermis a terminal meristem be-

comes organized. Vascular tissue differentiates back until a connection is made with that of the main stem. Soon a smooth juncture of cambiums of new and old stems comes about and the shoot continues its growth as would the original stem tip.

Shoots arising terminally involve a greater number of tissues. Most of them were found to arise from external callus produced by either the pith or the phloem (figs. 3*B*, 5, 6), and never a combination of the two. Cortex, xylem, cambium, and endodermis may also be involved with either pith or phloem to a small extent. Here, as in the lateral shoots, a complete tieup of new and old vascular tissues is effected, either directly as in figure 6, or indirectly as in figure 7. The meristematic areas seen clearly in the pith of the latter figures are connected directly with a large shoot above that level, and indirectly by means of vascular strands to the organized vascular system of the old stem below that level.

Control plants produce no mounds of callus tissue at the cut surface. On the contrary, more of the layers of pith cells beneath the cut die than do those over the other tissues, thus causing a sunken appearance in the center. Cell divisions in a horizontal plane occur, so that a weak phellogen is produced across the cut surface, which remains about as flat as at the time of decapitation.

UNWOUNDED AND WOUNDED FIRST INTERNODES.—A small daub of the 3 per cent mixture was placed on the first internodes just below the petiole of the first leaf of 28-day-old seedlings grown in soil. Care was taken not to injure the stem. Gross reactions of unwounded plants were somewhat faster than those of decapitated ones. Reaction occurred almost entirely below the point of application, very slightly above, and was not apparent laterally to any great extent. Under the application of the paste an elongated, narrow lesion appeared, which became sunken and brown, extending downward through the entire internode. Through this the more or less longitudinally regular rows of adventitious root primordia protruded by the end of 9 days. These did not elongate further under the conditions in which they were grown.

The fourth internodes of 45-day-old seedlings were encircled with an extremely fine band of the lanolin mixture. Here again the reac-

tion was limited almost completely to those portions of the stem below the site of application (fig. 1*D*). A definite swelling of the entire internode, which was first apparent within 24 hours, was soon extended downward through several internodes. Within 48 hours after treatment a pronounced whitening of the stem throughout the swollen portion occurred, followed within about a week by the production of root primordia.

Except for two features, the early stages of histological reactions were similar to those of decapitated plants. The activation of all tissues except the pith and the centripetal ends of the rays was the same as in that of decapitated plants. These two tissues, however, showed no response to the application (fig. 8*B*), and could not be distinguished from those of untreated plants. The second feature was the lack of protruding callus. If the treated part of the stem was not placed in a moist chamber, the rows of root primordia eventually became buried by a smooth mound of callus, and the lesion apparently healed over.

SEEDLINGS GROWN IN SAND: RESPONSES IN RELATION TO NITROGEN DEFICIENCY

Seedlings 40 days old which had been grown in sand and supplied with complete nutrient solution were separated into two groups, one of which was continued on the complete nutrient while the other was given the nutrient solution which lacked nitrates. Ten days later, which was at the time of treatment, the $-N$ plants tested negative to diphenylamine. They were lighter green in color, somewhat smaller in size, and a little woodier than the $+N$ ones. These differences became much more pronounced with the progress of the experiment, as can be seen by figure 1*A*, which shows a control plant of each group.

DECAPITATED PLANTS.—The $+N$ plants were decapitated between the seventh and eighth nodes, while the $-N$ ones, owing to their shorter height, were decapitated between the sixth and seventh nodes. This was as close to the top of the plant as it was possible to cut and get a smooth internode.

The general histological response pattern under both conditions of nutrition was the same, although differences were apparent in the growth rate and somewhat in the type of reaction of the different tissues involved.

At the time of treatment the average stem diameter of the $-N$ plants was about 15 per cent smaller than that of the $+N$ plants. The cortex of the latter was relatively wider and its pith was relatively very much larger than that of the former, the differences being ascribable to number of cells and not to cell size. Cell walls of the $-N$ plants, especially those of the pericyclic fibers, were heavier, the relative amount of vascular tissue was much greater, and the cambial activity was less than that of the $+N$ ones (fig. 8C, D).

By the end of 48 hours (fig. 9A) considerable cell divisions in the rays, primary phloem parenchyma, and endodermis, and some in the pith have occurred in the $+N$ plants, while in the others (fig. 9B) the only apparent response is a prominence of nuclei in the endodermis and rays.

Within 90 hours the root primordia of the $+N$ plants (fig. 9C) have been almost completely organized, while the cortex, endodermis, phloem, rays, and pith cells are all actively dividing. Mounds of callus tissue are appearing over the top of the cut surface. The tissues are about equally activated along all radii. The $-N$ plants of this age (fig. 9D) are not quite so far along in development as were the $+N$ plants in 48 hours, and their vascular cylinders are very unequally activated, large portions remaining unresponsive.

By 132 hours the ring of root primordia of the $+N$ plants (fig. 10B) has pushed out so far as completely to disrupt the cortex and epidermis. An inner ring of root primordia, derived from pith cells especially opposite the pith rays, are growing inward. This is not apparent in all the plants studied, however. Many circular vascular strands are forming in the rays between the protoxylem points (fig. 8A). On the other hand, root primordia of the $-N$ plants are not yet fully organized. Activity in the pith and cortex is much less pronounced, and divisions are confined mostly to rays, phloem, and endodermis (fig. 10A).

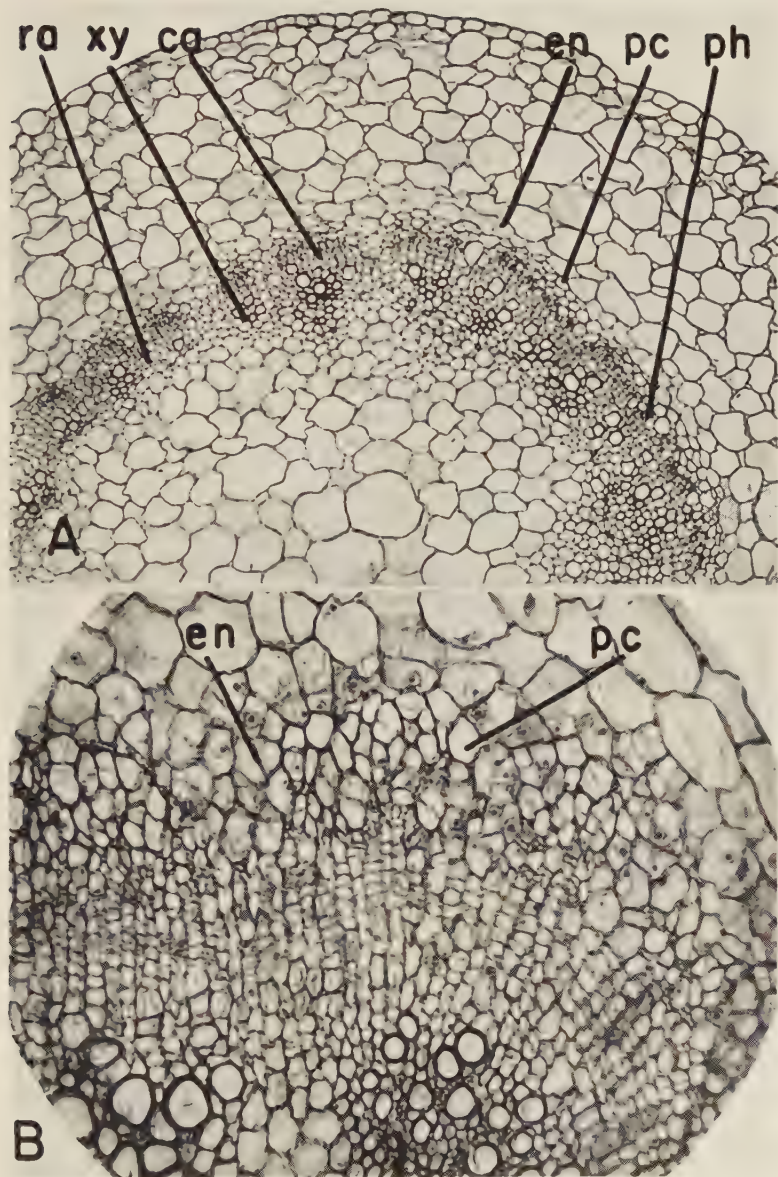


FIG. 2.—Decapitated first internodes of young plants in soil smeared with lanolin mixture. *A*: at time of treatment (*ra*, ray; *xy*, xylem; *ca*, cambium; *en*, endodermis; *pc*, pericycle; *ph*, phloem). *B*: 60 hours after treatment. Note activity in cambium, rays, endodermis, and phloem; and inactivity in pericycle.



FIG. 3.—*A*: 336 hours after treatment. Root primordia pushed out through epidermis and cortex. Note activity in periphery of pith. *B*: decapitated and treated first internode of plants grown in soil, 408 hours after treatment. Terminally produced shoot involving mostly cortex, also endodermis and phloem to some extent.

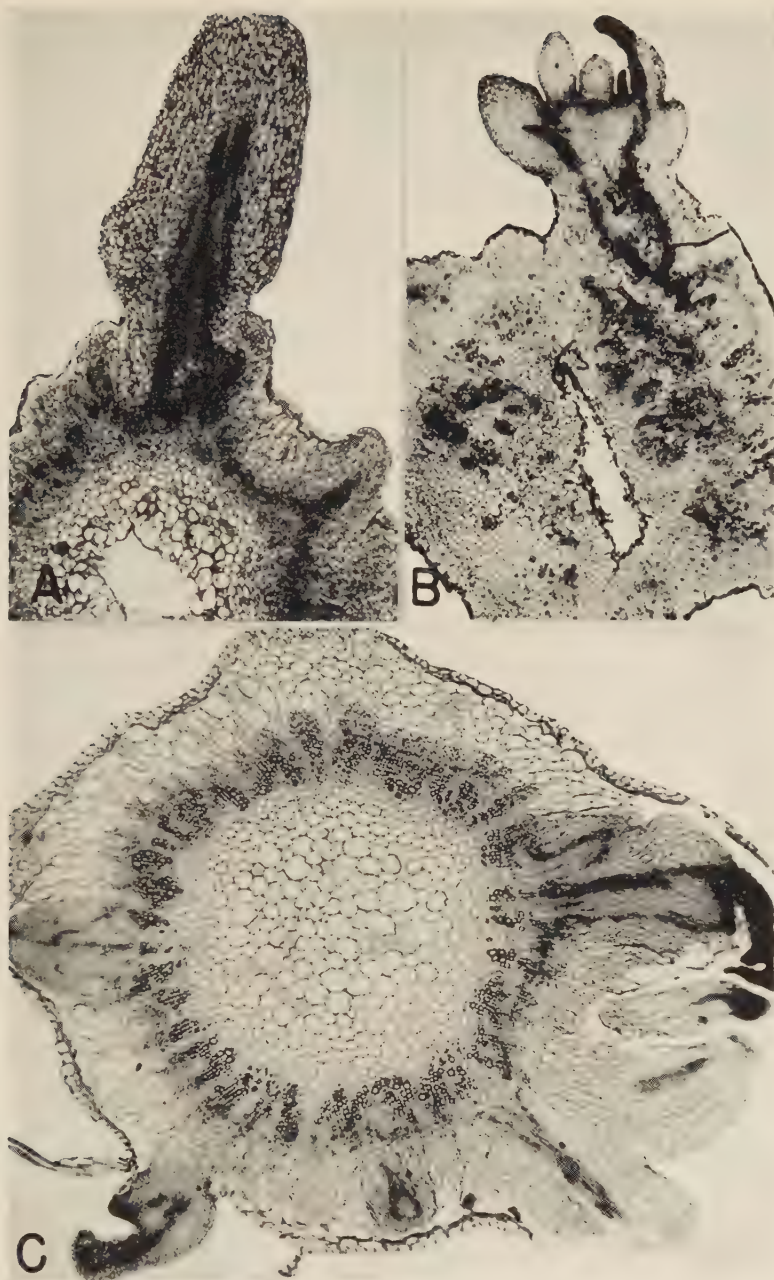


FIG. 4.—Decapitated and treated first internodes of plants grown in soil. *A*: 396 hours after treatment. Shoot produced laterally from cortex has established complete vascular connections with original stem. *B*: 408 hours after treatment. Shoot arising from callus developed over cortex has established vascular connections with vascular strands which in turn connect with vascular system of main stem. Note lack of callus developed over central part of pith and irregularity of maturation of vascular elements within callus. *C*: 396 hours after treatment. Two older shoots developed from cortex; two younger ones arising in same tissue.

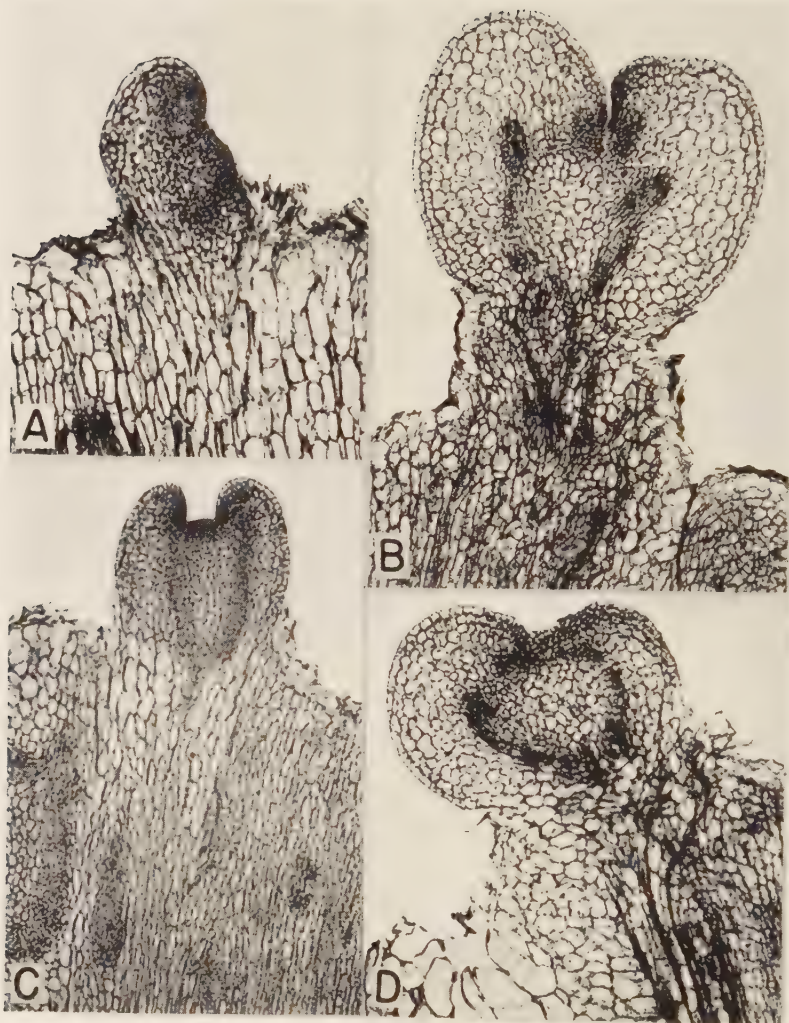


FIG. 5.—*A, B, C, D*: decapitated and treated first internodes of plants grown in soil. Shoots originating from callus produced over phloem.

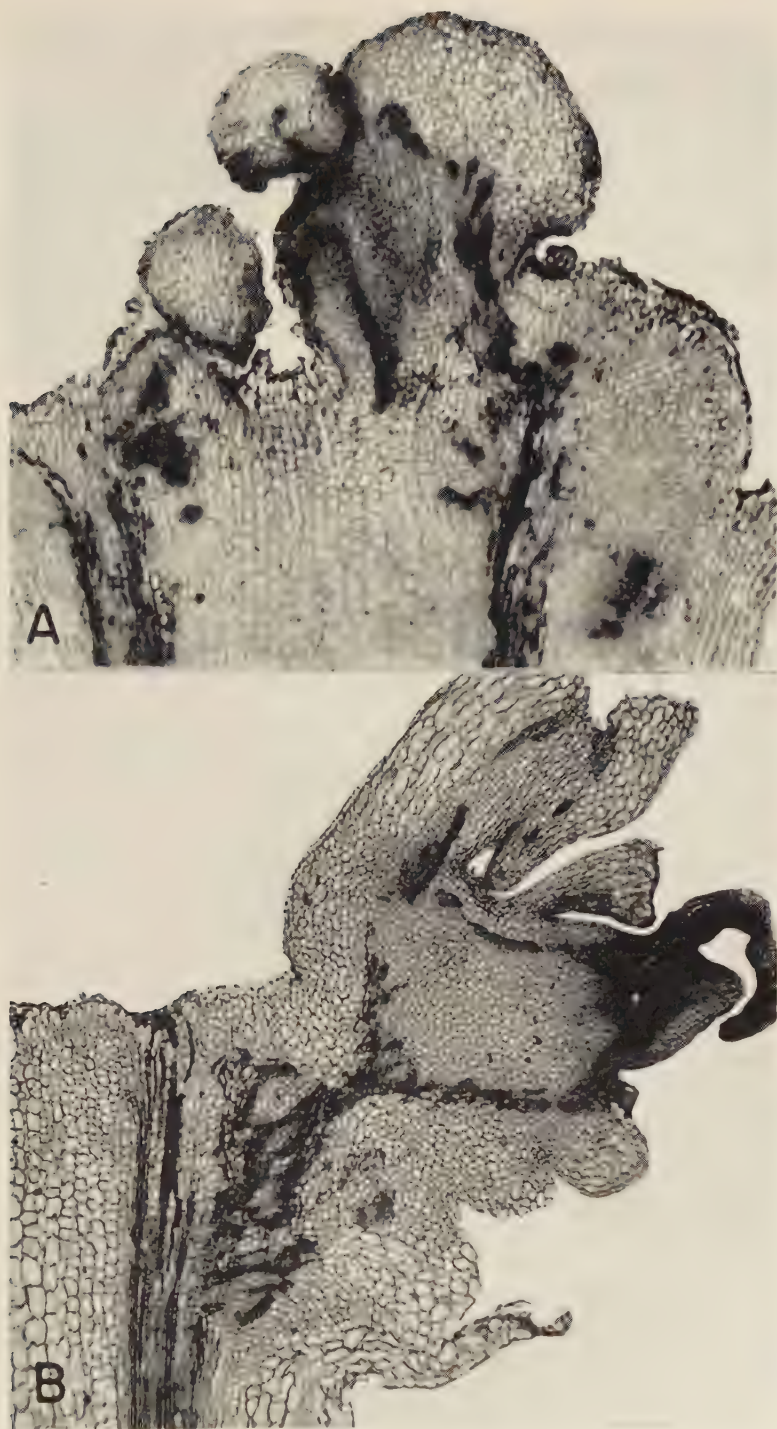


FIG. 6.—Decapitated first internodes of plants grown in soil and smeared with 3 per cent lanolin mixture. *A*: 288 hours after treatment; shoot produced from callus mostly over pith, with some involvement of xylem. *B*: 396 hours after treatment; shoot arising from phloem.

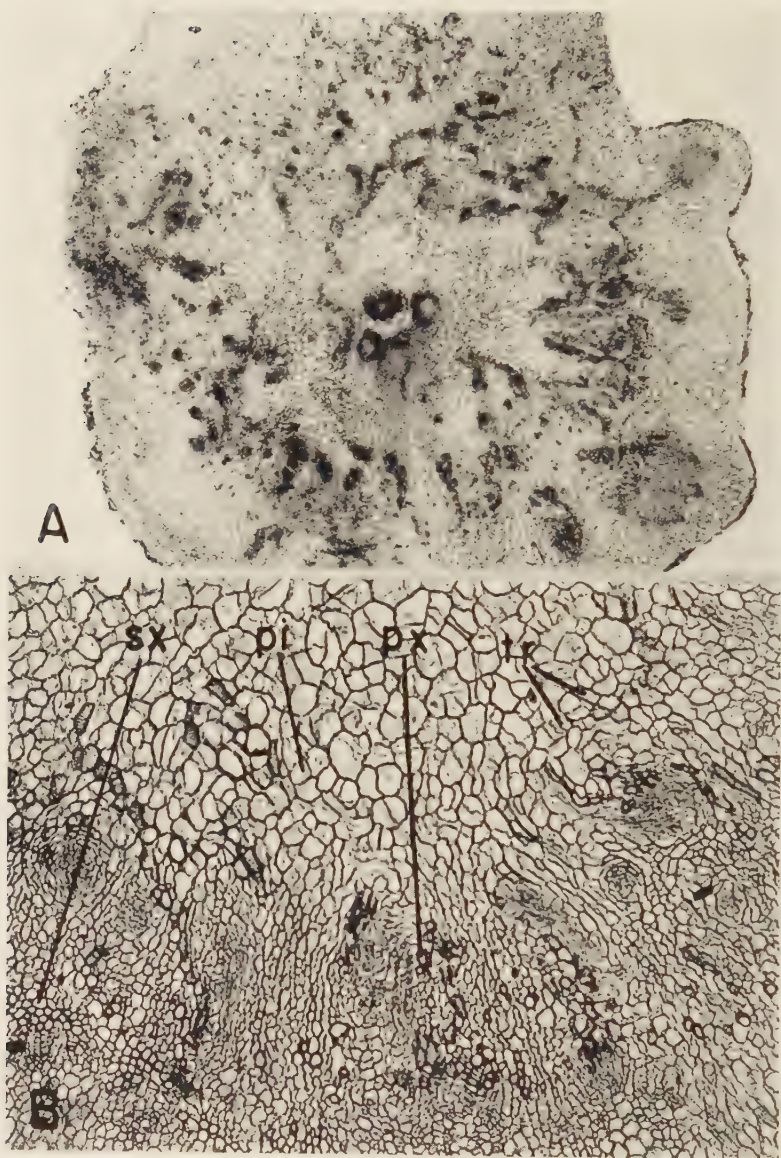


FIG. 7.—*A*: similar stem, 372 hours after treatment. Note great activity in pith, connecting above with a shoot, below with main stem. *B*: stem similar to that of *A*, one portion enlarged. Note development of vascular strands, maturation of irregularly oriented tracheids, and great numbers of cell divisions in pith.

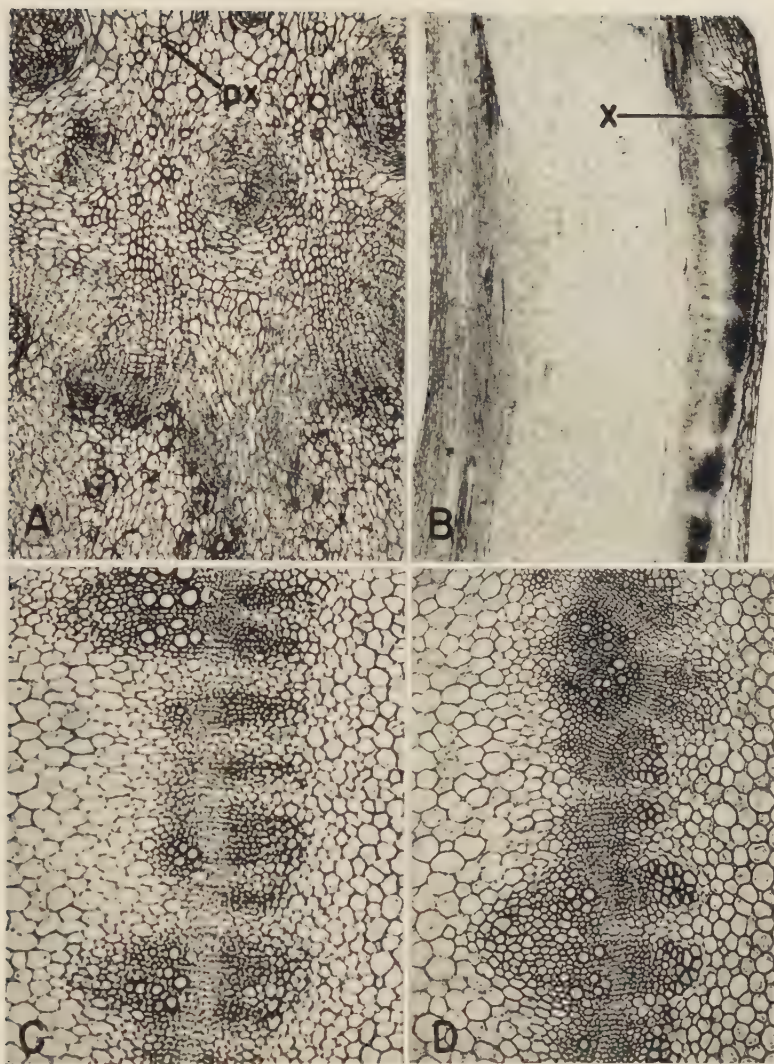


FIG. 8.—*A*: stem similar to that of fig. 7*A* and *B*, but at lower level and still further enlarged. *B*: unwounded first internode, treated by placing small daub of 3 per cent paste at *X*. Note most of activity below point of application and none on opposite side. *C*: +*N* plant, grown in sand, at time of treatment. *D*: –*N* plant, other conditions same as *C*. Diameter of entire stem of *C* actually more than twice that of *D*; therefore note lesser relative amount of vascular tissue in *C*, also its more active cambium, wider rays, and thinner walled pericyclic fibers than *D*.

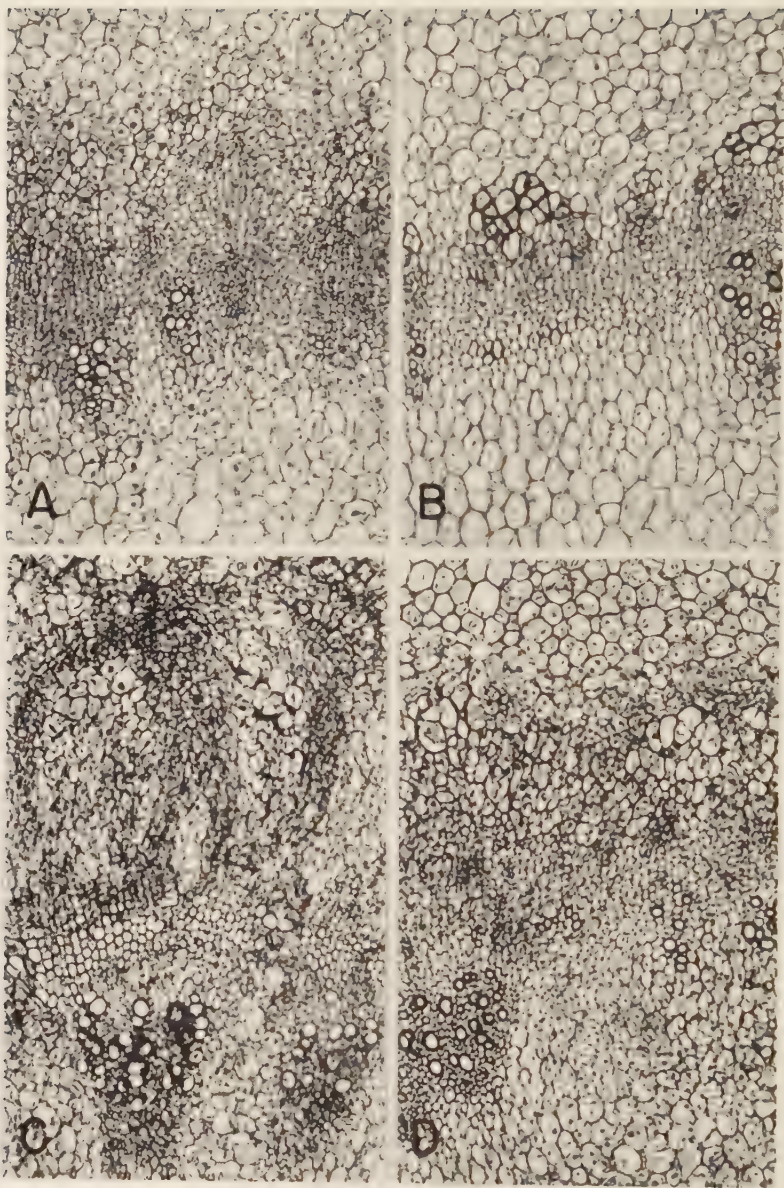


FIG. 9.—Plus N or -N plants decapitated near top of stem and smeared with 3 per cent lanolin mixture. *A*: +N, 48 hours after treatment. Great activity in rays, cambium, and phloem, some activity in endodermis and periphery of pith. *B*: -N, 48 hours after treatment. No change from time of treatment except prominence of nuclei in endodermis and rays. *C*: +N, 90 hours after treatment. Location of root primordia determined. Reactive tissues shown in *A* plus the cortex have proliferated extensively. *D*: -N, 90 hours after treatment. Large numbers of cell divisions in endodermis, rays, and cambium, some divisions in cortex and pith.

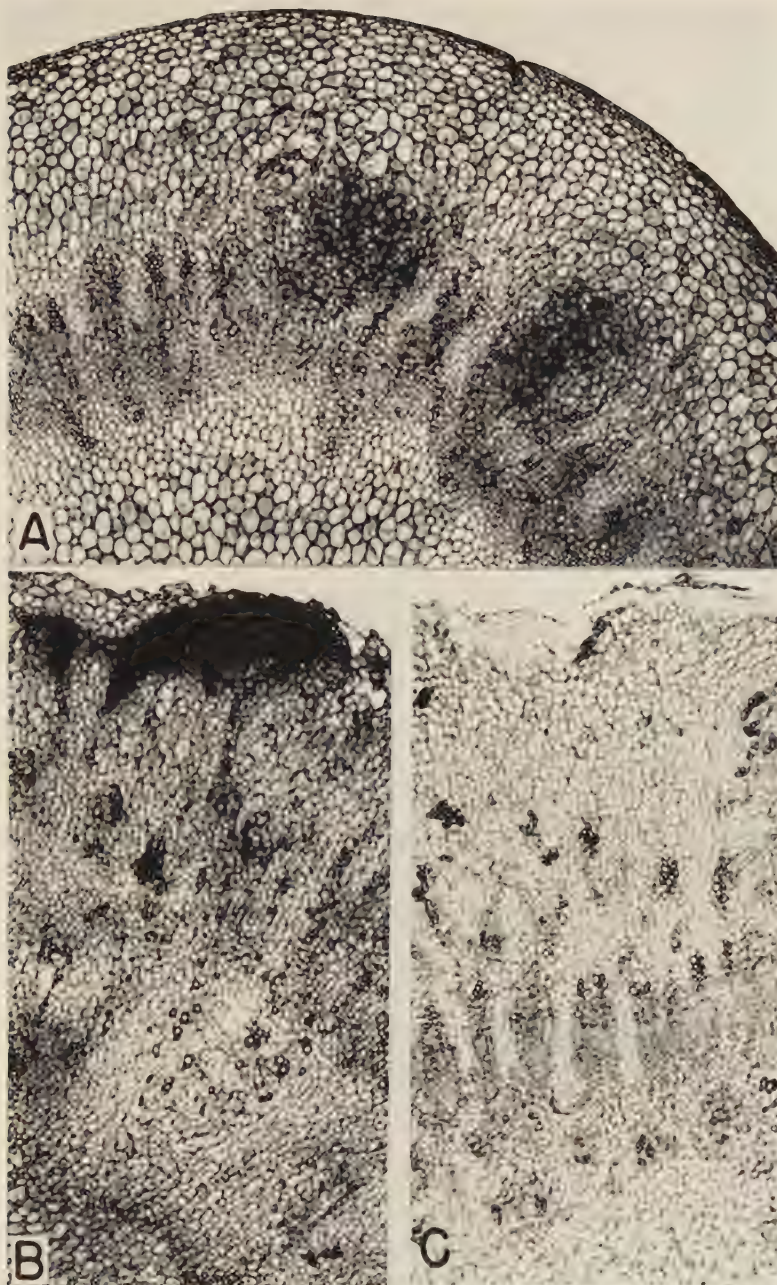


FIG. 10.—Plants similarly treated to those of fig. 9. *A*: -N, 132 hours after treatment. Root primordia just being organized. Note unequal activation of vascular cylinder and comparative inactivity of all tissues especially pith and cortex. *B*: +N, 132 hours after treatment. Note well developed root primordia, vascular strands, root primordia in pith, proliferation of xylem parenchyma which has pushed apart primary xylem elements. Epidermis and most of cortex gone. *C*: -N, 240 hours after treatment. Below level shown in *A*. Note scattered groups of fibers in cortex.

In final development (fig. 10C), the $-N$ plants produce very few, irregularly placed root primordia which rarely penetrate beyond the confines of the outer cortex and epidermis. Very little callus tissue is produced and this is less disorganized than the calluses of the $+N$ plants. The fewer meristematic patches are smaller in extent, tend to be tangential or radial rather than circular, are largely confined to the cortex and a short lateral extent in the pith; they are more regularly vascularized, producing complete vascular strands with phloem fibers, cambium, and xylem in the same relative relationship as in the original vascular cylinders.

Many patches of fibers are scattered throughout the cortex, where cortical cells have divided and their daughter cells have matured shortly thereafter. There is somewhat less tissue breakdown than is apparent in the $+N$ ones in which the phloem flanking the root primordia is disintegrating. Since the pith is not highly active, all of the innermost root primordia and many of the meristematic areas in the pith are lacking.

UNWOUNDED INTERNODES.—The unwounded internodes of $+N$ and $-N$ plants reacted relatively as did the decapitated ones, with no pith development occurring in either case. The root primordia of the $-N$ plants could rarely be induced to grow out, even when covered with moist sand. Figure 1B shows a $+N$ plant which had been covered by moist sand at the place of treatment so that the root primordia lengthened and became a functional part of the root system.

Discussion

The reaction of the cabbage plant to applications of the hormone is very similar to that of bean as described by KRAUS, BROWN, and HAMNER (9). Cabbage when untreated produces no mass of callus tissue over the cut surface. In this respect it is unlike the bean but similar to the tomato (2) and *Iresine* (8).

The epidermis and cortex of cabbage respond similarly to those of bean, tomato, *Iresine*, and *Mirabilis*. Endodermis of cabbage reacts in a manner similar to that of tomato and *Mirabilis*, being less active than that of bean and more so than that of *Iresine*. Pericycle

of cabbage is inactive, resembling bean and tomato in this respect. The vascular tissues differ in their responsiveness from those of *Mirabilis*, the latter being relatively unresponsive while those of the other three are sensitive to applications.

Adventitious root production in cabbage closely parallels that of bean, in that it involves mainly the rays plus proliferated phloem, and does not involve pericycle as do *Iresine* and *Mirabilis*. Cabbage pith is very active and produces large numbers of irregular vascular strands which in later stages extend into the center of the stem; this reaction is similar to that of bean, and differs from *Mirabilis* in that its activity is initiated very early.

Inhibition or at least retardation of bud growth has been reported in cases where decapitated plants have been treated with growth promoting materials. In cabbage, as in *Nicotiana* (5) and *Lilium* (1), however, indoleacetic acid has been found to facilitate adventitious bud production from centers which were not meristematic previous to the treatment. In cabbage, although not in the other two plants, the chemical treatment merely induces the internal conditions requisite for expression of a capacity which normally rarely comes to expression. Just what determines which ones of the plants will produce shoots, however, is not known. Apparently each plant has a certain capacity for reaction, and this may be expressed in either root or shoot production or both. If shoots are produced, then the number of adventitious roots is greatly reduced.

It has been repeatedly noted by various workers that older plants or older regions of plants do not respond to applications of indoleacetic acid so rapidly nor to so great an extent as do young ones. The rate of this response in cabbage has already been noted. This is undoubtedly due to the state of maturity of the cells involved. Highly vegetative or young plants have relatively less differentiation of tissue and therefore a lesser maturity of cells than have feebly vegetative or older ones (10).

In general, the tendencies of the applications of the indoleacetic acid and the lack of nitrogen are to produce opposite effects on the cells. The former tends to cause a delay of maturity or, if the cell is already matured, first a resumption by it of that capacity for

division which is characteristic of immature cells (dedifferentiation), and then division. The lack of nitrogen, on the other hand, tends to hasten maturity of the cells, which sharply limits their capacity for division. Since most of the cells of the stems to which applications were made responded by cell enlargement or cell division or both, this resulted in a lessening of the effect of the chemical agent on the $-N$ plants. This was expressed in fewer and slower cell divisions and a hastening of maturation after cell division, and therefore in a more limited amount of tissue involvement and in a lesser growth of new organs produced, such as root primordia. The lack of nitrogen hastened the maturity so greatly that the stimulated cells often divided only once or twice before maturing. This was particularly noticeable in the cortical cells. Many of those which were stimulated to divide matured into heavy walled fibers at once, resulting in many small scattered groups of those cells in the usually parenchymatous tissue. Thus in the $-N$ plants, even though the hormone was able to overcome to a certain extent the tendency of the lack of nitrogen to hasten maturation and to prevent dedifferentiation of cells, yet the effect of the latter condition was marked.

The cells of the highly vegetative plants, most of which were in a relatively less matured state and had an ample food supply, were able to respond more readily and to a greater degree through continued divisions of their derivatives.

From a study of cellular reactions of various tissues of any one plant under different conditions, and from a comparison of the reaction of tissues of that plant with the same tissues of other plants, it is evident that, although indoleacetic acid may be the particular incitant in each case, yet it is not more than one factor in a causal complex. Reactions of the plant to it are dependent upon the hereditary constitution of the plant and the environmental factors affecting it, together with its past experience and the correlative effects of one part upon another part (II).

The fact that the unwounded plants did not react to so great an extent as the decapitated ones may be ascribed to the difficulty of penetration through the heavily cuticularized walls of the epidermis.

Summary

1. Applications of a 3 per cent mixture of indole(3)acetic acid in lanolin were made to decapitated stems and to unwounded internodes of cabbage plants grown in ordinary greenhouse soil. Similar treatment was given to plants half of which were grown under conditions of high nitrogen nutrition, the other half with a depletion of nitrogen.

2. Observations were made over a period of several weeks. The decapitated, soil-grown plants responded grossly by the production of masses of callus and root primordia.

3. All tissues of the stem responded to some extent to the treatment. The most generally responsive tissues were those of the phloem, rays, and pith. Cambium, cortex, endodermis, and xylem were moderately stimulated, while the epidermis and pericycle reacted weakly.

4. Adventitious roots were developed from ray and phloem tissue. Some internal roots were produced from pith cells adjacent to the primary xylem.

5. Near the surface of application confused mounds of callus tissue derived mainly from phloem and pith produced irregular groups of meristematic tissues in which great numbers of tracheids matured.

6. About one-third of the plants produced viable shoots, either directly from the top of the callus or laterally at about the level of adventitious root production. These lateral shoots were initiated by cell divisions either in the central or innermost cell layers of the cortex or in the rays, and always established organic union with vascular tissue of the main stem.

7. Stems treated laterally produced sunken areas through which in later stages the root primordia protruded. No mounds of callus were produced. No activity was apparent in the pith, but all other tissues reacted proportionally the same though to a less extent than in decapitated plants.

8. The reaction was slower in the $-N$ plants than in the $+N$

ones. They produced a much smaller callus, through which the root primordia rarely protruded.

9. The same tissues were involved in reactions of both +N and -N plants, although to a lesser extent in the latter. The pith and cortex of the -N plants were less active than in the +N ones, most divisions being confined to the rays, phloem, and endodermis. These, although the most active tissues in the -N stems, were still not nearly so reactive as those in the +N ones. The small amount of callus produced was less confused and showed greater vascularization than did that of the +N plants. Maturation of many cells, formerly parenchymatous, into fibers was characteristic.

10. Since the entire vascular cylinder was very unequally activated in the -N plants, far fewer root primordia were produced. These rarely grew out far enough to penetrate through cortex and epidermis.

The writer is indebted to the members of the botany department of the University of Chicago for helpful suggestions made during the course of this study.

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